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Neural Evolution: Marginal Gains through Soma Location

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Unlike in most vertebrate neurons, the soma of many arthropod and mollusc neurons is placed at the end of a thin neurite. Multi-compartment computational modelling suggests this strategy may reduce the attenuation of signals from the dendrites, reducing the energy costs of signalling.

Since the earliest neuroanatomists revealed the morphology of single neurons from vertebrates and invertebrates over 100 years ago [1,2], a striking difference has been obvious: neurons in vertebrate brains typically have their soma interposed between their dendrites and axon (Figure 1A), whereas in the neurons of many invertebrates, such as arthropods and molluscs, the soma is placed at the end of a thin neurite (Figure 1B). In these invertebrate neurons the dendrites are in close proximity to the site of action potential initiation, linking directly to the axon [3]. The reason for this difference in morphology has been unclear but a new study by Hesse and Schreiber [4] in this issue of *Current Biology* demonstrates that by improving the efficiency of signal propagation an externalised soma may be advantageous over a central soma in some circumstances.

Hesse and Schreiber [4] compared the possible implications of a centralised or externalised soma using computational models of single neurons. Used in this way, computational modelling can be an invaluable tool for exploring the possible designs and configurations of biological systems. It is especially useful for studying systems such as single neurons in which the consequences of changing specific parameters can be quantified in functionally relevant ways (e.g., [5,6]). Using this approach, comparisons can be made among an array of designs with different combinations of parameters. Many such combinations may not exist, or have ever existed, in an actual biological system but their properties can still be quantified and compared. By coupling this approach with parameters measured from actual biological systems it is possible to determine the regions of parameter space that these systems occupy, revealing the inefficiencies inherent in certain parameter combinations and even biophysical constraints (e.g., [5,6]).

The alternative neural morphologies with a central or externalised soma were instantiated in multi-compartment computational models (Figure 1C,D) [4]. Such models approximate the morphology of neural dendrites and axons as a series of linked electrical compartments, each of which incorporates the basic biophysical membrane properties. The size and shape of each of these compartments can be altered, and they can be populated with various types of voltage-gated ion channels that modify their electrical

properties. Hesse and Schreiber [4] use three distinct types of model, a passive model with properties defined by membrane resistance, axial resistivity and capacitance, an active model populated with voltage-gated Na^+ and K^+ channels, and an analytical formula that captures the behaviour of the passive model.

Using these models, Hesse and Schreiber [4] quantified the effect of soma size and position on signals propagating from the dendrite to the axon by determining the minimal amplitude of a dendritic input necessary to produce a specific voltage threshold in the axon. Interposed between dendrite and axon, a central soma attenuates passive signals, a larger soma causing greater attenuation. This can be mitigated by placing the soma at the end of a stem neurite though some attenuation still occurs due to the additional membrane needed for the stem neurite; the thicker the stem neurite, the greater the attenuation. Thus, if the soma is large or the stem neurite thin then external placement is favourable because it reduces signal attenuation. Hesse and Schreiber [4] support this conclusion with published data on the morphology and electrophysiology from neurons of various species showing that those with an externalized soma tend to have a higher soma-to-neurite ratio than those with a central soma.

Why is reducing signal attenuation beneficial? The voltage-gated Na^+ and K^+ channels in the region of the axon proximal to the soma add noise to signals transmitted from the dendrites [7–9]. For signals attenuated by a large soma this noise will be relatively larger than for signals less attenuated by a small soma or a narrow stem neurite. So, reducing the attenuation of signals from the dendrites is beneficial because it improves the signal-to-noise ratio. Indeed, additive channel noise substantially reduces the information content of graded signals reaching the spike initiation zone [9]. Yet as Hesse and Schreiber [4] point out, reduced attenuation can be interpreted not only in terms of information processing but also energy consumption. They argue that when there is little attenuation less energy must be invested to amplify dendritic signals to ensure they are large enough to overcome additive noise and contribute to spike generation.

Energy is a vital commodity for biological systems, influencing all aspects of their design and behaviour [10]. The energy consumption of neural tissue is particularly high as a consequence of the ion fluxes across the cell membrane needed to generate graded electrical signals and spikes [11,12]. Sodium–potassium ATPases in neurons must do work to pump ions back across the membrane consuming considerable amounts of energy, even when neurons are at rest [11,12]. Consequently, animals are likely to be under strong selective pressure to reduce neuronal energy consumption [12]. Indeed, numerous features of nervous systems from the biophysics of single neurons to the placement of brain regions are thought to have been influenced by the need to reduce energy consumption [7,9,11,12]. So, energy reduction may have been a selective pressure promoting a shift in soma position to the end of the stem neurite [4].

Yet energy is not the only commodity of value for biological systems: multiple selective pressures may act in similar or opposing directions. Indeed, a large soma interposed between dendrites and axon would affect the conduction delay and frequency content of signals from the dendrites, which may be costly. In this case, externalising the soma would simultaneously reduce the conduction delay and increase the frequency bandwidth of signals from the dendrites while also reducing energy consumption. For a small soma, however, the effects on the conduction delay and bandwidth will be less pronounced, while energy consumption may be increased by externalisation. Thus, for large somata several selective pressures may act in concert to promote externalisation, while there may be opposing selective pressures acting on small somata.

This is not the first recent attempt to explain the differential positioning of the soma in vertebrate and arthropod (or mollusc) neurons; an earlier study by Rivera-Alba and colleagues [13] also published in *Current Biology* tackled a similar though not identical problem. While Hesse and Schreiber [4] considered soma location in the context of a single neuron, Rivera-Alba and colleagues [13] considered whether somata are distributed within or separated from the neuropile, the region of the nervous system containing the dense aggregation of dendrites, axons and synapses. To explain these different arrangements they adopted the approach of minimising the total length of neuronal wiring [14,15], the idea being that the neuronal 'wires', the dendrites and axons, are themselves costly in terms of several factors, including conduction delays, signal attenuation and energy. Consequently, reducing the amount of neuronal wire also reduces conduction delays, attenuation and energy consumption. Adopting this approach, Rivera-Alba and colleagues [13] showed

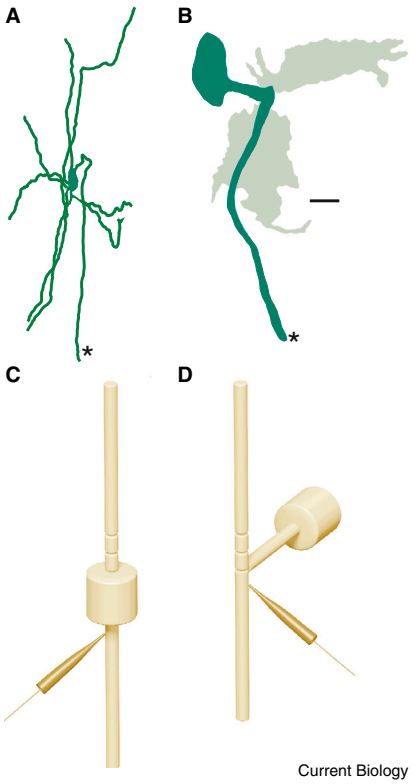

Figure 1. The position of the soma differs among vertebrate and invertebrate neurons.
(A) A superior cervical cell from the hamster. Dark green shows soma, dendrites and axon (marked with an asterisk). Redrawn from [20]. (B) A motor neuron from the ventral nerve cord of the desert locust. Dark green shows soma, stem neurite and axon (marked with an asterisk). Pale green shows the extent of dendritic ramification. Scale bar is 50 microns. Redrawn from [3]. (C) A multi-compartment model of a neuron with the soma interposed between dendrite and axon [4]. (D) A multi-compartment model of a neuron with the soma located at the end of a stem neurite, and a direct connection between dendrite and axon [4].

that whether cell bodies are segregated or embedded within neuropile depends upon the relative volume of the soma and the stem; a larger soma favouring the segregated arrangement.

Together the studies of Hesse and Schreiber [4] and Rivera-Alba and colleagues [13] demonstrate that there are good reasons why large somata are typically found at the ends of stem neurites rather than interposed between dendrites and axon, and are often segregated from the neuropile. These studies [4,9] have made considerable progress in explaining why neurons from different animal phyla have such different morphologies. Yet they are far from the final word on such differences, and numerous questions remain unanswered. For example, although the studies [4,13] tell us which arrangements are favourable for large or small somata, they do not explain why such differences in size exist. The giantism of the somata of some mollusc neurons may be necessary to support greater pre-synaptic function [16], an explanation that may also account for giantism of the somata of some arthropod neurons. Yet this is only a partial explanation because it doesn't explain why vertebrate neurons do not show similar giantism.

Another puzzle is why when somata do become extremely small in arthropods, as they do in the smallest insects and spiders [17–19], their positions do not switch from external to central. In these cases the entire nervous system has undergone miniaturisation, so it is possible that the relative size of the stem neurite remains relatively smaller so that there would be no reason to switch. However, another possibility is that a developmental constraint prevents these arthropods from switching unipolar neurons to bipolar or multipolar neurons within short evolutionary timescales. Whatever the answers to these and the many other questions that abound, the differences between vertebrate and invertebrate nervous systems will continue to intrigue scientists for many years yet.

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Cell Division: Molecular Pathways for KMN Kinetochore Recruitment

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Robust but dynamic attachment between kinetochores and spindle microtubules is an essential prerequisite for accurate chromosome segregation and for preventing aneuploidy. A pair of recent studies has shed light on the details of how the molecular machinery that orchestrates these attachments is recruited to mitotic kinetochores.

The separation of duplicated sister chromatids into two new daughter cells during mitosis is accomplished by the attachment of microtubules to chromosomes. Kinetochores, a hierarchal assembly of ~100 proteins formed at the centromeric region of chromosomes, are the sites where these attachments are formed and maintained [1]. The KMN network, comprised of the Knl1, Mis12

